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Artículo Original

TEMPORAL SEGREGATION BETWEEN TWO ARMADILLO SPECIES IN THE SOUTHERN PANTANAL OF BRAZIL

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ABSTRACT. The Pantanal of Brazil is the largest tropical wetland in the world and home to a high diversity of armadillos, with up to six sympatric species in any one location. Among these species are the nine-banded armadillo (*Dasypus novemcinctus*) and six-banded armadillo (*Euphractus sexcinctus*), both highly specialized diggers. We investigated how these two armadillos partitioned resources and coexisted by exploring multiple aspects of their ecology, including diel activity through camera trapping, and substrate and microhabitat preference through burrow sampling in forest and grassland habitats. Ultimately, we found no significant differences between the substrate particle sizes in two habitats (forest and grassland). However, because we could not confirm the relationship between burrows and species, the data obtained in the field were not sufficient to determine these correlations. We found a significant difference in activity patterns between the species, with nine-banded armadillos exhibiting greater nocturnal activity and six-banded armadillos exhibiting more diurnal activity. The species overlapped minimally overall in their activity patterns, with the highest amount of overlap occurring at dusk. Our study suggests temporal segregation occurs between these two armadillos and may serve as an ecological strategy to reduce competitive interactions between them. Future studies would benefit from assessing alternative niche axes between or among two or more armadillo species in other ecoregions.

RESUMO. SEGREGAÇÃO TEMPORAL ENTRE DUAS ESPÉCIES DE TATUS NO SUL DO PANTANAL DO BRASIL. O Pantanal brasileiro é a maior planície alagável do mundo e apresenta alta diversidade de tatus, com seis espécies simpátricas. Dentre estas espécies estão duas de tamanho semelhante, o tatu-galinha (*Dasypus novemcinctus*) e o tatu-peba (*Euphractus sexcinctus*), ambos cavadores altamente especializados. Investigamos como essas duas espécies de tatus partilham recursos e coexistem, explorando múltiplos aspectos da ecologia das espécies, incluindo atividade diária com dados de armadilhas fotográficas e preferência de substratos e micro-habitats através da análise de tocas em ambientes de florestas e campos. Em última análise, não encontramos diferença significativa no tamanho das partículas do substrato entre os dois tipos de habitat (florestas e campos). Entretanto, como não conseguimos confirmar a relação entre tocas e espécies, os dados obtidos em campo não foram suficientes para determinar essas correlações. Encontramos diferença significativa nos padrões de atividade entre as duas espécies, com tatus-galinha exibindo mais atividade noturna, enquanto os tatus-peba exibiram mais atividade diurna. As espécies apresentaram um mínimo de

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sobreposição dos períodos de atividade, com a maior porção desta ocorrendo ao anoitecer. Nosso estudo sugere que a segregação temporal ocorre entre essas duas espécies de tatu e pode servir como uma estratégia ecológica para reduzir interações competitivas entre elas. Estudos futuros se beneficiariam da avaliação de eixos de nicho alternativos entre duas ou mais espécies de tatus em outras ecorregiões.

Key words: Cingulata, coexistence, diel activity, ecology, Pantanal.

Palavras-chaves: Atividade diária, Cingulata, coexistência, ecologia, Pantanal.

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INTRODUCTION

Examples of niche partitioning can be found across the globe in a variety of taxa and ecological systems. Species often partition resources as a means of reducing competition and thus promoting long-term co-occupation of the same areas (Rosenzweig & Sterner 1970; Schoener 1974; Wilson & Yoshimura 1994; Gravel et al. 2011). Hutchinson (1957) established that species with high overlap in certain niche dimensions often cannot coexist. Resource partitioning to reduce dietary overlap is a common strategy seen in a variety of species. Rosenberger (1992) showed that the high diversity of New World primates likely occurs through extensive dietary zones, with different species consuming different sources and proportions of food, including exudate (tree sap), insects, nuts, fruits, and leaves, depending on body size. Additionally, two species of Neotropical opossum have been shown to spatially segregate when their dietary overlap is significant (Kuhnen et al. 2017).

Time or diel activity is another niche axis that can often be partitioned to facilitate coexistence (Schoener 1974; Wilson & Yoshimura 1994). Temporal segregation is a common behavioral mechanism that reduces competition if there is already substantial overlap in diet and space (Schoener 1974; Di Bitetti et al. 2010). Camera trapping is a useful technique to measure activity patterns among species and can provide evidence to support temporal segregation (Frey et al. 2017). Using camera traps, researchers have documented temporal segregation among mammalian carnivores in tropical forests (Di Bitetti et al. 2010), high-elevation deserts (Lucherini et al. 2009), and tropical wetlands (Bianchi et al. 2010). Although most mammals exhibit a broad range of activity (Refinetti 2008), flexibility in activity preference is broadly distributed among nocturnal, diurnal, and cathemeral species (Cox et al. 2021).

To achieve coexistence between or among species, high overlap on any niche axis is usually accompanied by avoidance on another axis (Stewart et al. 2003). In North America, mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and introduced cattle (*Bos taurus*) all exhibit low overlap in their diet during the summer, despite significant overlap in habitat use (Stewart et al. 2002, 2003). In South America, two species of brocket deer in the Atlantic rainforest exhibit similar space use patterns but also segregate temporally (Ferreguetti et al. 2015). Of course, it is possible for there to be minimal overlap in multiple niche dimensions, even for closely related species with similar distribution ranges such as the maned wolf (*Chrysocyon brachyurus*), crab-eating fox (*Cerdocyon thous*), and hoary fox (*Lycalopex vetulus*), all of which differ sufficiently in diet, habitat use, and activity patterns in the Brazilian Cerrado (Jacomo et al. 2004) to support coexistence.

The Pantanal is the largest tropical wetland in the world (Alho et al. 1988) and is located predominantly in the Brazilian states of Mato Grosso and Mato Grosso do Sul. With more than 150 species of mammals, this region is one of South America's important biodiversity hotspots (Tomas et al. 2010). The tropical wetlands of central-western Brazil are home to a high diversity of armadillos, with up to six extant sympatric species (Desbiez et al. 2022). Armadillos are New World mammals that currently comprise at least 21 species (Wetzel 1985; Vizcaíno & Milne 2002; Wilson & Mittermeier 2018) of the two families Dasypodidae and Chlamyphoridae (Order Cingulata) (Wilson & Mittermeier 2018).

Within this diverse Order are two similarly-sized species: the nine-banded armadillo (*Dasypus novemcinctus*) and the six-banded armadillo (*Euphractus sexcinctus*). Nine-banded armadillos have the largest geographic distribution among all armadillos, with four described species ranging from the southern United States to northern Argentina (Barthe et al.

2024). They occupy a variety of habitats, including temperate and tropical forests, savannas, grasslands, wetlands, and even anthropogenically disturbed habitats (e.g., pastures, ranches, urban areas) (Loughry et al. 2014). The six-banded armadillo is relatively widely distributed (Abba et al. 2014) and found in forests, savannas, grasslands, and wetlands (Abba et al. 2014). The distribution of both species overlaps across Brazil except for the Amazon Basin (Eisenberg & Redford 1999; Loughry et al. 2014; Ferreguetti et al. 2016).

The presence of these two species across Brazil poses unique questions in terms of how similar species might coexist. Prior studies of armadillos suggest they have very diverse diets, with six-banded armadillos believed to be more carnivorous (Redford 1985; Dalponte & Tavares-Filho 2004) than the nine-banded armadillo, which is an insectivorous generalist (Redford 1985, 1986). However, dietary overlap does occur with respect to the consumption of insects, and if so, this might suggest the possibility of niche partitioning on another axis to facilitate coexistence.

Armadillos also exhibit extreme morphological adaptations to their fossorial habits (Vizcaíno et al. 1999; Vizcaíno & Milne 2002), and differences in morphology likely contribute to their coexistence. Among the 21 known species, all are different with respect to their limb morphology; some species are more cursorial (i.e., limbs adapted for running), whereas others are strongly fossorial or demonstrate intermediate adaptations, such as when digging is not essential as an alimentary strategy (Vizcaíno et al. 1999). Differences in morphology may also prove to be important predictors of substrate preference, as more powerful diggers might, for example, burrow in tougher substrate, and vice versa. Despite being members of different families, both nine-banded and six-banded armadillos fall into the same "in-between" category (demonstrating intermediate adaptations for fossoriality) (Vizcaíno et al. 1999), yet they preferentially burrow in different habitats. In the Atlantic rainforest of Brazil, nine-banded armadillo burrows were commonly found in swamps and forested habitats, whereas six-banded armadillos preferred open habitats (Ferreguetti et al. 2016). Furthermore, they tend to burrow into or around termite mounds in the Cerrado (Carter & Encarnação 1983). If substrate differs among habitats, then it could be indicative of species presence. Furthermore, because some species can be identified by the dimensions of their burrows (Carter & Encarnação 1983), substrate and burrow size might aid in understanding the habitat preference for armadillos.

Finally, if two armadillo species exhibit overlap in space and/or dietary niches, they may partition resources temporally (i.e., through differences in diel activity). Assessments of activity patterns are frequently used in studies assessing niche differentiation, but few of these studies have addressed armadillos, possibly due to their fossorial habits or more secretive and elusive nature. In the Atlantic rainforest of Brazil, six-banded and nine-banded armadillos exhibit contrasting activity patterns, with the latter being more diurnal and the former being more nocturnal (Ferreguetti et al. 2016). The same is true in the Brazilian Pantanal, with the most overlap occurring in the early evening (Maccarini et al. 2015). As the Pantanal is mostly privately owned and with many cattle ranches in the surrounding area (Seidl et al. 2001), understanding how wildlife can coexist with human presence may be especially important. Our study thus provides yet another opportunity to further explore the relationship between these two species but in more disturbed habitats. The aim of this study is to assess the ecological (realized) niche of six-banded and nine-banded armadillos by estimating their activity patterns through camera trapping and evaluating habitat preferences through analyses of burrow location and substrate conditions. We hypothesize that the species will exhibit differences in substrate preference and/or activity time/period.

MATERIALS AND METHODS

Study area

Fazenda San Francisco (FSF) is a 90 km² private ranch where cattle raising, agriculture, and wildlife observation activities are performed (20°5.2'S, 56°36.9'W) (**Fig**. 1). It is located between highway BR 262 and Miranda River in the Pantanal, Brazil. Although the ranch is situated primarily in the southern portion of the Brazilian Pantanal, it is in an ecotone between the Pantanal and Cerrado biomes. Ranch land use is diverse, and FSF is composed of cow pastures, irrigated rice fields, roads, broad forest patches, savanna formations, and wetlands. Six-banded and nine-banded are the only two armadillos recorded on the ranch.

Habitat and substrate preference

We surveyed and sampled open fields and forest patches. We sampled substrate in pastures and native forest patches within this area (see **Fig**. 1) by walking systematically to locate armadillo burrows and then comparing the substrates of armadillo burrows in both habitats. Burrows were more visible for direct location in open field areas but were also identified by the presence of nearby armadillos, the identification of tracks at/near an entrance, and through

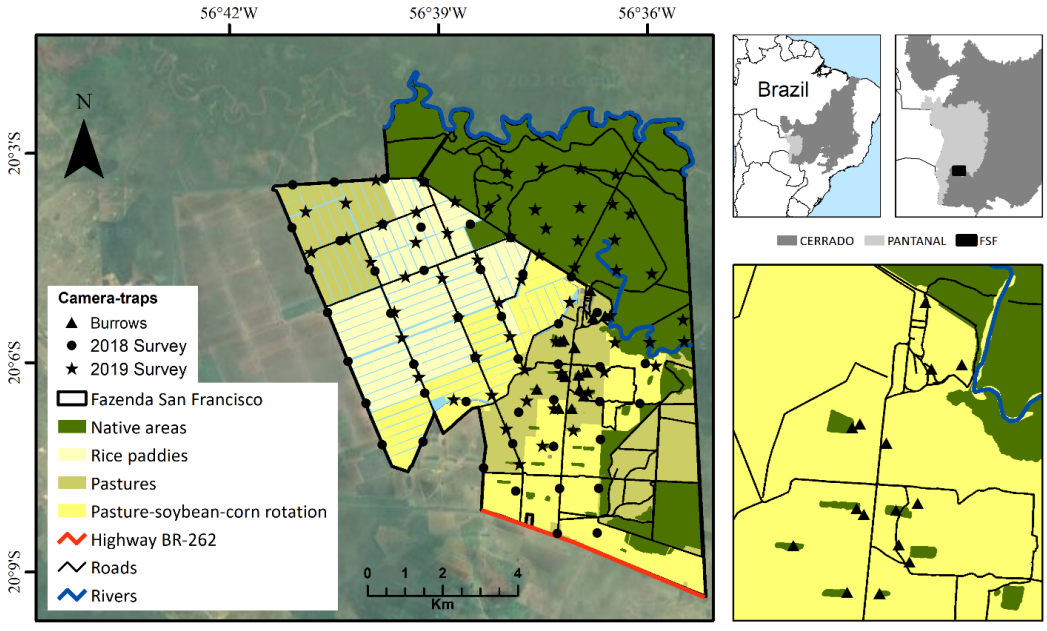

Fig. 1. Fazenda San Francisco (FSF) cattle-wildlife ranch and ecotourism lodge located in the southern Brazilian Pantanal showing land use and land cover classes and the location of camera-traps used in the present study. In the bottom right the location of camera-traps installed in armadillo burrows.

the use of camera traps. We assumed that camera-traps could help us identify those species creating burrows, so we devised a method to potentially determine if there were differences in substrate preferences between the two species. We measured several aspects of these burrows, including height (cm), width (cm), depth (cm), aspect (degrees) of burrow entrances, as well as distance (cm) to the nearest insect mound. We planned to identify which species dug any unidentified burrows by using the dimensions of the entrance as well. Searches for insect mounds were conducted within a 50 m radius of the burrow once it was discovered. In the two cases where no insect mound was found within a 50 m radius, we recorded the distance as double the maximum distance found at all other mounds.

To evaluate differences in substrate, we dug holes adjacent to each burrow to a depth of 40 cm (McDonough et al. 2000) and extracted 1 kg of soil by scraping the edges from the top to the deepest portion. Each sample was then run through a set of sieves that segregated the soil by the following grain sizes: 5 mesh/4 mm, 10 mesh/2 mm, 35 mesh/0.5 mm, 60 mesh/0.25 mm, and 120 mesh/0.125 mm and less. The mass (g) of each soil partition was then recorded (g) to determine the percentage of particles in each size category.

To assess the potential for habitat differences between species, we classified burrow habitat as either "open" (i.e., characterized by open plains and cow pastures) or "forest" (i.e., characterized by the presence of trees and arboreal vegetation cover). We assigned these by using a principal component analysis (PCA) to visualize the variables (e.g., location, substrate size of each sieve partition, height, width, depth, aspect, distance to insect mound) in multidimensional space (Bro & Smilde 2014). All variables were converted to *z*-scores before integration into a PCA. Finally, we used a perMANOVA to test for differences between open fields and forest patches among the same suite of variables (Anderson 2017).

We used camera traps (Reconyx HyperFire 2 HF2X) to identify the species associated with burrow occupancy and assess overall wildlife activity around burrows. We deployed eight camera traps in front of fresh/recent burrows in forested and open areas. Cameras were positioned 1 m away from each burrow, were active at each location for 10-12 days, and were then moved to different burrows to sample more areas. The sampling period ranged from 3 July 2019 to 6 August 2019. Burrows were chosen based on evidence of recent activity, including the presence of a dirt mound at the entrance, a lack of spiderwebs or debris blocking the entrance, or visual confirmation of individuals entering. Data collected from these cameras is included in our activity pattern analysis.

Activity patterns

We used camera traps (ScoutGuard SG565F, CuddeBack E-model, Reconyx HyperFire HC 500) to assess differences in activity patterns between the two armadillo species. Data came from two ongoing surveys of mammal communities that were also occurring in the study area. The first survey was conducted between October and December 2018, when 63 camera-trap stations were established across a sampling area of 50 km^2. The second survey occurred in 2019 between July and December when 60 camera-trap stations were deployed to cover a 50 km^2 sampling area. For both surveys,

camera-traps were placed no closer than 1 km apart and distributed across the sampling area in proportion to the habitat types present. Every month we checked and removed any vegetation or debris in front of the devices that could interfere with their proper functioning. These data were then combined with data gathered from the substrate and habitat preference camera-trap surveys and were evaluated together. Because the two species of armadillos are very similar in size and behavior, we assumed that any changes in detection rates across habitats would be similar for them both and hence would not affect the broad patterns we are looking at.

Activity patterns for each species were evaluated using the R packages "camtrapR" (Niedballa et al. 2016) and "Activity" (Rowcliffe 2016). Activity for each animal was estimated from presence/absence records and based on the time stamp of each photo capture. If multiple photos of the same species occurred less than 1 hour apart, then only the first photograph was included to avoid pseudoreplication (Linkie & Rideout 2011; Porfirio et al. 2016b). A Watson's two-sample homogeneity test was used to evaluate for significant differences between activity patterns for both species. To assess the degree of overlap in activity between species, we used the overlap coefficient Dhat4 from the R package "Overlap" (Rideout & Linkie 2009), which ranges from 0 (no overlap) to 1 (complete overlap), and it performs better when the smaller of the two samples is larger than 50 observations (Rideout & Linkie 2009).

RESULTS

Habitat and substrate preference

We measured and sampled 26 burrows: 14 in open fields and 12 in forest patches. Unfortunately, we could correctly identify only eight burrows to species level, and all were six-banded armadillos. Nine-banded and six-banded armadillos were the only species directly entering all the recorded burrows. All but two burrows were found within a 50 m radius of an insect mound. The PCA explained little variation among the variables, with PC1 explaining 25.3 % of variation and PC2 explaining 17.9 % variation (**Fig**. 2). Given we could not identify which species made each burrow, we cannot conclude whether or not there was a preference; however, there was no difference in the distribution of particle sizes among the burrows (F_1=1.48, P=0.22), suggesting no species preference or that all or most burrows were dug by only one of the species.

Activity patterns

We logged a total of 5710 camera-trap nights during the three separate wildlife surveys. They included a total of 120 independent records of the six-banded armadillo and 121 independent records of the nine-banded armadillo. We found that activity patterns between species differed significantly (U^2=2.201, P<0.05), with six-banded armadillos exhibiting more diurnal activity peaking around 12:00 h and a second smaller peak at 19:00 h. Nine-banded armadillos exhibited more nocturnal activity, with activity peaking around 19:00 h and a second peak at 01:00 h. Both species exhibited minimal overlap in activity (*Dhat4* = 0.42), with the highest amount of overlap occurring at around 19:00 h (**Fig**. 3).

DISCUSSION

We predicted the substrate analysis might provide another axis of segregation, but the results were inconclusive because we could not identify the burrows' original digger. Burrows were commonly found on the ranch, but the only burrows we identified conclusively belonged to six-banded armadillos. Further research on substrate preference might prove more fruitful once burrows can be identified to the actual digger.

Camera-traps provided evidence of nine-banded armadillos using burrows originally inhabited or dug by six-banded armadillos. For example, one camera trap regularly recorded activity at a burrow actively occupied by a six-banded armadillo. On 8 July 2019 at 15:26 h, a six-banded armadillo was seen entering the burrow. However, on the same day at 16:02 h, a nine-banded armadillo was seen entering the same burrow, only to quickly retreat (**Fig**. 4). This same behavior was recorded the following day (9 July 2019) at 18:46 h. Later, a six-banded armadillo was detected entering the burrow, followed hours later by a nine-banded armadillo (10 July 2019 01:44 h), which again exited almost immediately. On 25 July 2019 at a different camera trap station, a six-banded armadillo was seen leaving its burrow at 18:58 h. This vacant burrow was then entered by a nine-banded armadillo at 19:07 h, which remained inside for two minutes. Despite this behavior, nine-banded armadillos are known to frequently dig and abandon their own burrows in Brazil (McDonough et al. 2000), and this behavior might extend to other species as well. However, it is unknown if the individual nine-banded armadillos we observed were foraging or if they were searching for a new burrow to use. Furthermore, other armadillos have also been observed using the burrows of sympatric species (Desbiez & Kluyber 2013; Rodrigues et al. 2020).

In our study, nine- and six-banded armadillos exhibited temporal segregation in the study area, with six-banded armadillos active more during the day and nine-banded armadillos active largely in the evening. Our results are consistent with the findings of similar studies in the Pantanal (Maccarini et al.

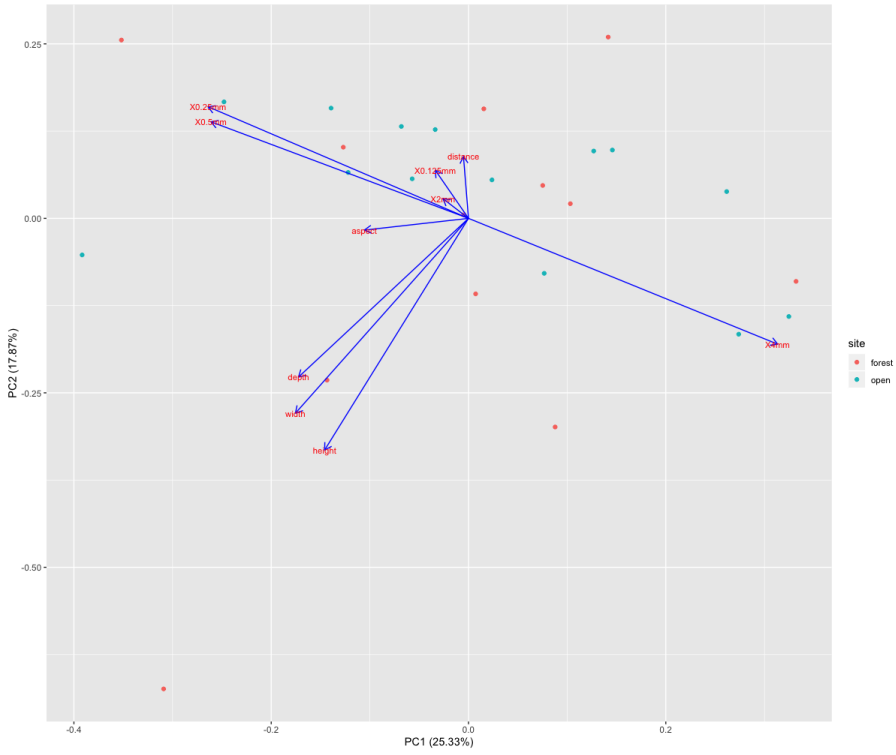

Fig. 2. PCA (converted to z-scores) explains minimal variation among burrow variables between sites; the percent variation accounted for by each PC in parentheses.

2015), with species exhibiting high overlap during the onset of the evening (i.e., at around 19:00 h). Temperature is also known to influence the activity of both species (Maccarini et al. 2015), and this may have also contributed to the differences in activity patterns between these two species. Armadillos are often only active for short durations and spend a lot of time thermoregulating inside their burrows (McDonough & Loughry 1997). Six-banded armadillos appear to be physiologically adapted to warmer temperatures, which may explain their activity peaks during the hottest hours of the day (Maccarini et al. 2015). In contrast, nine-banded armadillos are active during a narrower range of temperatures, which might explain their more nocturnal habits in the Pantanal (Maccarini et al. 2015). Given that armadillos have naturally low metabolic rates (Maccarini et al. 2015), physiological studies may prove to be even more useful in understanding these adaptations, as it is likely that air temperature plays a crucial role in the activity of both species, with burrows acting as thermal shelters (Maccarini et al. 2015; Attias et al. 2018).

Among potentially competing predator species, diel activity has been known to relate to prey activity (Kronfeld-Schor & Dayan 2003). At Fazenda San Francisco, the presence of large carnivores such as jaguars (*Panthera onca*), pumas (*Puma concolor*), and maned wolves might also influence armadillo activity. In certain areas of the Pantanal, jaguars, and pumas have significant overlap in their activity patterns (Porfirio et al. 2016a) and among potential prey items (Crawshaw & Quigley 2002; Porfirio et al. 2016a). In Belize during the evening, the nocturnal nine-banded armadillo is frequently preyed upon by jaguars and opportunistically preyed upon by pumas (Harmsen et al. 2010). The nine-banded armadillo also appears to be less active during a full moon, potentially as a method of reducing encounters with predators (Harmsen et al. 2010). In the Pantanal, where jaguars are more diurnal than in other parts of their range, they also consume large prey such as capybaras (*Hydrochoerus hydrochaeris*) (Crawshaw & Quigley 1991; Harmsen et al. 2010). However, because both jaguars and pumas prey upon a wide diversity of medium- to larger-bodied mammals

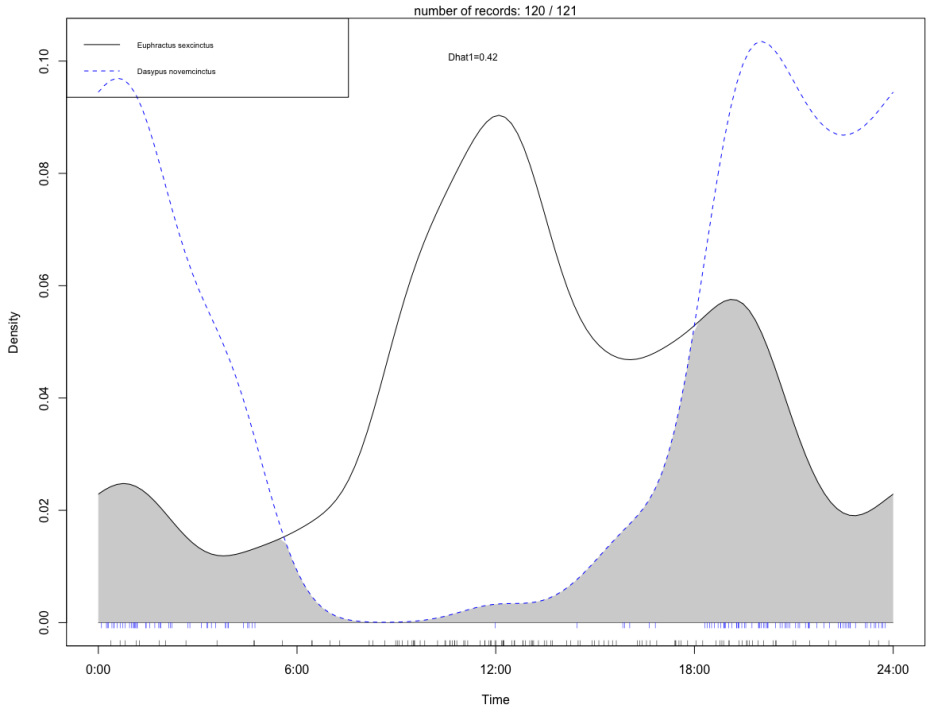

Fig. 3. Activity patterns between the six-banded armadillo (*Euphractus sexcinctus*) and nine-banded armadillo (*Dasypus novemcinctus*). Tic marks below the graph are actual records of occurrence and the shaded area is overlap between species.

Fig. 4. Six-banded armadillo (*Euphractus sexcinctus*) (A) and nine-banded armadillo (*Dasypus novemcinctus*) (B) using the same burrow.

(Aranda & Sanchez-Cordero 1996; Scognamillo et al. 2003; Harmsen et al. 2010), their activity might not influence armadillos. Likewise, whereas the maned wolf is known to consume both species of armadillo (Cartes et al. 2013), it also consumes a large number of fruits and plant matter (Bueno & Motta-Júnior 2004; Jacomo et al. 2004), so its predation on armadillos might be more opportunistic.

Although smaller carnivores, such as ocelots (*Leopardus pardalis*) and crab-eating foxes, occur at higher densities than large carnivores in our study area, their presence may not have a strong influence on the temporal activity of both armadillo species. Both crab-eating foxes and ocelots are known to consume armadillos in other ecosystems and locations (Bueno & Motta-Júnior 2004; Abreu et al. 2008; Bianchi et al. 2010), but this alone might not be enough to influence armadillo activity patterns. Ocelots usually prey on smaller mammals, such as rodents and marsupials, although they will also take

primates (Abreu et al. 2008; Bianchi et al. 2010); likewise, the crab-eating fox is much more of a generalist and often consumes more plant matter than animal matter (Jacomo et al. 2004).

Besides minimizing predation risk, armadillos may time activity to coincide with the availability of their primary prey or decrease interactions with sympatric species. For example, the naked-tailed armadillo (*Cabassous unicinctus*) and six-banded armadillo exhibit strong diel activity overlap in the Pantanal, but dietary preferences are dissimilar (Redford 1985; Desbiez et al. 2018). In contrast, in the Brazilian Cerrado, six-banded and nine-banded armadillos exhibit overlap in their diet (Anacleto 2007). Six-banded armadillos have a broad, omnivorous diet that includes ants (Hymenoptera), beetles (Coleoptera), termites (Isoptera), as well as other orders within the class Arthropoda, including moths and butterflies (Lepidoptera); grasshoppers, crickets, and katydids (Orthoptera); spiders (Araneae); and centipedes (Chilopoda). Unlike nine-banded armadillos, they also consume vertebrates such as frogs and toads (Anura) and reptiles (Squamata) (Anacleto 2007). At the same study site, nine-banded armadillos exhibited a less diverse diet, with relatively equal consumption of ants, termites, and beetles. However, they consumed a higher diversity of termite species (5) than six-banded armadillos (Anacleto 2007). The consumption therefore of different termite species by nine-banded armadillo, combined with a lack of consumption of alternative species (e.g., chilopods, spiders, vertebrates), suggests dietary overlap is minimal. However, because the dietary preferences of both species were not studied here, this would benefit from further investigation.

When considering the diversity and the ecological overlap among sympatric armadillo species, coexistence likely arises through various means. Because nine-banded and six-banded armadillos exhibit overlap in morphology (Vizcaíno et al. 1999) and dietary preferences (Redford 1985; Anacleto 2007) across their geographical ranges, niche segregation on another niche axis may potentially be facilitating their coexistence (Stewart et al. 2003). Our study showed that activity patterns between the two armadillo species are significantly different, with some overlap in secondary activity peaks at dusk. Our results are thus consistent with the idea that temporal segregation may be an efficient ecological strategy to maintain coexistence between these two species across their range.

Despite the diversity of order Cingulata, armadillos have not been intensively studied (Loughry et al. 2015; Rodrigues et al. 2020), and many species are listed as IUCN "threatened" or "data deficient" (Superina et al. 2014). Yet because their presence and functioning in ecosystems may have long-term benefits for many sympatric wildlife species, it is critical more investments be made in understanding the ecology and behavior of these species. As a final consideration, we know that instances of niche segregation are not always indicative of competition. Species may segregate over time due to several factors, many of which are outside the control of researchers (Connor & Simberloff 1986). Given the vast diversity of biomes and ecotones in the Neotropics, it is likely that many factors have contributed to the adaptive radiation among mammalian species across this large biogeographical region. We sought to understand the relationship between two species by exploring observable niche dimensions and evaluating evidence supporting one or more competition or niche segregation mechanisms.

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LITERATURE CITED

Abba, A. M., E. Lima, & M. Superina. 2014. *Euphractus sexcinctus*. The IUCN Red List of Threatened Species 2014: e.T8306A47441708. https://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS.T8306A47441708.en

Abreu, K. C., R. F. Moro-Rios, J. E. Silva-Pereira, J. M. D. Miranda, E. F. Jablonski, & F. C. Passos. 2008. Feeding habits of ocelot (*Leopardus pardalis*) in Southern Brazil. Mammalian Biology 74:407-411. http://dx.doi.org/10.1016/j.mambio.2007.07.004

Alho, C. J., T. E. Lacher, & H. C. Goncalves. 1988. Environmental degradation in the Pantanal ecosystem. Bioscience 38:164-171. http://dx.doi.org/10.2307/1310449

Anacleto, T. C. S. 2007. Food habits of four armadillo species in the Cerrado area, Mato Grosso, Brazil. Zoological Studies 46:529-537.

Anderson, M. J. 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). Wiley StatsRef: Statistics Reference Online. https://doi.org/10.1002/9781118445112.stat07841

Aranda, M., & V. Sanchez-Cordero. 1996. Prey spectra of jaguar (*Panthera onca*) and puma (*Puma concolor*) in tropical forest of Mexico. Studies on Neotropical Fauna and Environment 31:65-67. http://dx.doi.org/10.1076/snfe.31.2.65.13334

Attias, N., L. G. R. Oliveira-Santos, W. F. Fagan, & G. Mourão. 2018. Effects of air temperature on habitat selection and activity patterns of two tropical imperfect homeotherms. Animal Behaviour 140:129–140. http://dx.doi.org/10.1016/j.anbehav.2018.04.011

Barthe, M. et al. 2024. Exon capture museomics deciphers the nine-banded armadillo species complex and identifies a new species endemic to the Guiana Shield. Systematic Biology syae027. https://doi.org/10.1093/sysbio/syae027

Bianchi, R., S. L. Mendes, & P. D. Júnior. 2010. Food habits of the ocelot, *Leopardus pardalis*, in two areas in southeast Brazil. Studies on Neotropical Fauna and Environment 45:111-119. http://dx.doi.org/10.1080/01650521.2010.514791

Bianchi, R., N. Olifers, M. E. Gompper, & G. Mourao. 2016. Niche partitioning among mesocarnivores in a Brazilian wetland. PLoS One 11:9.

Bro, R., & A. K. Smilde. 2014. Principal component analysis. Analytical Methods 6:2812-2831. http://dx.doi.org/10.1039/c3ay41907j

Bueno, A. D., & J. C. Motta-Júnior. 2004. Food habits of two syntopic canids, the maned wolf (*Chrysocyon brachyurus*) and the crab eating fox (*Cerdocyon thous*), in southeastern Brazil. Revista Chilena de Historia Natural 77:5-14. http://dx.doi.org/10.4067/s0716-078x2004000100002

Carter, T. S., & C. D. Encarnação. 1983. Characteristics and use of burrows by four species of armadillos in Brazil. Journal of Mammalogy 64:103-108. http://dx.doi.org/10.2307/1380755

Cartes, J. L., A. J. Giordano, & N. M. Mujica Cameroni. 2013. The maned wolf (*Chrysocyon brachyurus*) in Paraguay. Ecology and Conservation of the Maned Wolf: Multidisciplinary Perspectives. (A. Consorte-McCrea, & E. F. Santos, eds). CRC Press, Taylor and Francis Publishing, Boca Raton, USA. http://dx.doi.org/10.1201/b15607-24

Crawshaw Jr., P. G., & H. B. Quigley. 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. Journal of Zoology 223:357-270. http://dx.doi.org/10.1111/j.1469-7998.1991.tb04770.x

Crawshaw Jr., P. G., & H. B. Quigley. 2002. Jaguar and puma feeding habits in the Pantanal, Brazil, with implications for their management and conservation. El jaguar en el nuevo milenio. (R. A. Medellin, C. Chietkiewicz, K. H. Redford, J. G. Robinson, E. Anderson, & E. A. Taber, eds.). Ediciones Científicas Universitarias, México.

Connor, E. F., & D. Simberloff. 1986. Competition, scientific method, and null models in ecology: Because field experiments are difficult to perform, ecologists often rely on evidence that is nonexperimental and that therefore needs to be rigorously evaluated. American Scientist 74:155-162.

Cox, D. T. C., A. S. Gardner, & K. J. Gaston. 2021. Diel variation in mammals associated with expanded trait space. Nature Communications 12:1753. http://dx.doi.org/10.1038/s41467-021-22023-4

Dalponte, J. C., & J. A. Tavares-Filho. 2004. Diet of the yellow armadillo, *Euphractus sexcinctus* in south-central Brazil. Edentata 6:37-41. http://dx.doi.org/10.1896/1413-4411.6.1.37

Desbiez, A. L. J., & D. Kluyber. 2013. The role of giant armadillos (*Priodontes maximus*) as ecosystem engineers. Biotropica 45:537-540. http://dx.doi.org/10.1111/btp.12052

Desbiez, A. L. J., G. F. Massocato, D. Kluyber, & R. C. F. Santos. 2018. Unraveling the cryptic life of the southern naked-tailed armadillo, *Cabassous unicinctus squadmicaudis* (Lund 1845), in a Neotropical wetland: Home range, activity pattern, burrow use and reproductive behaviour. Mammalian Biology 91:95-103. http://dx.doi.org/10.1016/j.mambio.2018.02.006

Desbiez, A. L. J., D. Kluyber, G. F. Massocato, L. G. R. Oliveira-Santos, & N. Attias. 2019. Spatial ecology of the giant armadillo *Priodontes maximus* in Midwestern Brazil. Journal of Mammalogy 101:151-163. http://dx.doi.org/10.1093/jmammal/gyz172

Desbiez, A. L. J., D. Kluyber, G. F. Massocato, L. M. Barreto, & N. Attias. 2022. What do we know about the armadillos of the Pantanal? Review of knowledge about their ecology, biology, morphology, health, conservation, distribution and study methods. Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais 17:11-69. http://dx.doi.org/10.46357/bcnaturais.v17i1.834

Di Bitetti, M., C. D. De Angelo, Y. E. Di Blanco, & A. Paviolo. 2010. Niche partitioning and species coexistence in a Neotropical felid assemblage. Acta Oecologica 36:403-412. http://dx.doi.org/10.1016/j.actao.2010.04.001

Di Blanco, Y. E., A. L. J. Desbiez, D. Di Francescantonio, & M. S. Di Bitetti. 2020. Excavations of giant armadillos alter environmental conditions and provide new resources for a range of animals. Journal of Zoology 311:227-238. http://dx.doi.org/10.1111/jzo.12782

Eisenberg, J. F., & K. H. Redford. 1999. Mammals of the Neotropics—the central Neotropics: Ecuador, Peru, Bolivia. University of Chicago Press, Chicago, USA. http://dx.doi.org/10.2307/3803112

Ferreguetti, A. C., W. M. Tomas, & H. G. Bergallo. 2015. Density, occupancy, and activity pattern of two sympatric deer (*Mazama*) in the Atlantic Forest, Brazil. Journal of Mammalogy 96:1245-1254. http://dx.doi.org/10.1093/jmammal/gyv132

Ferreguetti, A. C., W. M. Tomas, & H. G. Bergallo. 2016. Density and niche segregation of two armadillo species (Xenarthra: Dasypodidae) in the Vale Natural Reserve, Brazil. Mammalian Biology 81:138-145. http://dx.doi.org/10.1016/j.mambio.2015.10.007

Fontes, B. et al. 2020. The local extinction of one of the greatest terrestrial ecosystem engineers, the giant armadillo (*Priodontes maximus*), in one of its last refuges in the Atlantic Forest, will be felt by a large vertebrate community. Global Ecology and Conservation 24: e01357. https://doi.org/10.1016/j.gecco.2020.e01357

Frey, S., J. T. Fisher, A. C. Burton, & J. P. Volpe. 2017. Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. Remote sensing in ecology and conservation 3:123-132. http://dx.doi.org/10.1002/rse2.60

Gravel, D., F. Guichard, & M. E. Hochberg. 2011. Species coexistence in a variable world. Ecology Letters 14:828-839. http://dx.doi.org/10.1111/j.1461-0248.2011.01643.x

Harmsen, B. J., R. J. Foster, S. C. Silver, L. E. T. Ostro, & C. P. Doncaster. 2010. Jaguar and puma activity patterns in relation to their main prey. Mammalian Biology 76:320-324. http://dx.doi.org/10.1016/j.mambio.2010.08.007

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415-427. http://dx.doi.org/10.1101/sqb.1957.022.01.039

Jacomo, A. T. A., L. Silveira, & J. A. F. Diniz-Filho. 2004. Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Ducicyon thous*), and the hoary fox (*Dusicyon vetulus*) in central Brazil. Journal of Zoology 262:99-106. http://dx.doi.org/10.1017/s0952836903004473

Kronfeld-Schor, N., & T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics 34:153-181. http://dx.doi.org/10.1146/annurev.ecolsys.34.011802.132435

Kuhnen, V. V., G. Q. Romero, A. X. Linhares, & J. Vizentin-Bugoni. 2017. Diet overlap and spatial segregation between two neotropical marsupials revealed by multiple analytical approaches. PLoS ONE 12: e0181188. http://dx.doi.org/10.1371/journal.pone.0181188

Linkie, M, & M. S. Rideout. 2011. Assessing tiger-prey interactions in Sumatran rainforests. Journal of Zoology 284:224-229. http://dx.doi.org/10.1111/j.1469-7998.2011.00801.x

Loughry, J., C. McDonough, & A. M. Abba. 2014. *Dasypus novemcinctus*. The IUCN Red list of Threatened Species 2014:e.T6290A47440785. https://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS.T6290A47440785.en

Loughry, W. J., M. Superina, C. M. McDonough, & A. M. Abba. 2015. Research on armadillos: a review and prospectus. Journal of Mammalogy 96:635-644. http://dx.doi.org/10.1093/jmammal/gyv005

Lucherini, M. et al. 2009. Activity pattern segregation of carnivores in the High Andes. Journal of Mammalogy 90:1404-1409. http://dx.doi.org/10.1644/09-mamm-a-002r.1

Maccarini, T. B., N. Attias, I. M. Medri, J. Marinho-Filho, & G. Mourão. 2015. Temperature influences the activity patterns of armadillo species in a large neotropical wetland. Mammal Research. http://dx.doi.org/10.1007/s13364-015-0232-2

McDonough, C. M., & W. J. Loughry. 1997. Influences on activity patterns in a population of nine-banded armadillos. Journal of Mammalogy 78:932-941. http://dx.doi.org/10.2307/1382953

McDonough, C. M., M. J. DeLaney, P. Q. Le, M. S. Blackmore, & W. J. Loughry. 2000. Burrow characteristics and habitat associations of armadillos in Brazil and the United States of America. Revista de Biologia Tropical 48:109-120.

Niedballa, J., R. Sollman, A. Courtiol, & A. Wilting. 2016. camtrapR: an R package for efficient camera trap data management. Methods in Ecology and Evolution 7:1457-1462. http://dx.doi.org/10.1111/2041-210x.12600

Porfirio, G., P. Sarmento, V. Foster, & C. Fonseca. 2016a. Activity patterns of jaguars and pumas and their relationship to those of their potential prey in the Brazilian Pantanal. Mammalia. http://dx.doi.org/10.1515/mammalia-2015-0175

Porfirio, G., V. C. Foster, C. Fonsesca, & P. Sarmento. 2016b. Activity patterns of ocelots and their potential prey in the Brazilian Pantanal. Mammalian Biology 81:511-517. http://dx.doi.org/10.1016/j.mambio.2016.06.006

Redford, K. H. 1985. Food habits of armadillos (Xenarthra: Dasypodidae). The evolution and ecology of armadillos, sloths, and vermilinguas (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, DC, USA. http://dx.doi.org/10.1126/science.233.4768.1102

Redford, K. H. 1986. Dietary specialization and variation in two mammalian myrmecophages (variation in mammalian myrmecophagy). Revista Chilena de Historia Natural 59:201-208.

Refinetti, R. 2008. The diversity of temporal niches in mammals. Biological Rhythm Research 39:173-192. http://dx.doi.org/10.1080/09291010701682690

Rideout M., & M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statisitcs 14:322-337. http://dx.doi.org/10.1198/jabes.2009.08038

Rodrigues, T. F, A. M. B. Mantellatto, M. Superina, & A. G Chiarello. 2020. Ecosystem services provided by armadillos. Biological Reviews 95:1-21. http://dx.doi.org/10.1111/brv.12551

Rosenberger, A. L. 1992. Evolution of Feeding Niches in New World Monkeys. American Journal of Physical Anthropology 88:525-562. http://dx.doi.org/10.1002/ajpa.1330880408

Rosenzweig, M. L., & P. W. Sterner. 1970. Population Ecology of Desert Rodent Communities: Body Size and Seed-Husking as Bases for Heteromyid Coexistence. Ecology 51:217-224. http://dx.doi.org/10.2307/1933657

Rowcliffe, M. 2016. Animal Activity Statistics. R package version 1.3. https://CRAN.R-project.org/package=activity

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Scognamillo, D., I. E. Maxit, M. Sunquist, & J. Polisar. 2003. Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan Ilanos. Journal of Zoology 259:269-279. http://dx.doi.org/10.1017/s0952836902003230

Seidl, A. F., J. S. V. Silva, & A. S. Moraes. 2001. Cattle ranching and deforestation in the Brazilian Pantanal. Ecological Economics 36:413-425. http://dx.doi.org/10.1016/s0921-8009(00)00238-x

Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, & B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: Resource partitioning and competitive displacement. Journal of Mammalogy 83:229-244. http://dx.doi.org/10.1093/jmammal/83.1.229

Stewart, K. M., R. T. Bowyer, J. G. Kie, B. L. Dick, & M. Ben-David. 2003. Niche partitioning among mule deer, elk, and cattle: Do stable isotopes reflect dietary niche? Ecoscience 10:297-302. http://dx.doi.org/10.1080/11956860.2003.11682777

Superina, M., N. Pagnutti, & A. M. Abba. 2014. What do we know about armadillos? An analysis of four centuries of knowledge about a group of South American mammals, with emphasis on their conservation. Mammal Review 44:69-80. http://dx.doi.org/10.1111/mam.12010

Tomas, W. M., N. C. Caceres, A. P. Nunes, E. Fischer, G. Mourao, & Z. Campos. 2010. Mammals in the Pantanal wetland, Brazil. The Pantanal: Ecology, Biodiversity and Sustainable Management of a Large Neotropical Seasonal Wetland (W. J. Junk, C. J. Silva, C. N. Cunha, & K. M. Wantzen, eds.). Pensoft Publishers, Sofia, Bulgary. http://dx.doi.org/10.1007/978-94-007-4001-3_129

Vale, M. M. et al. 2023. Ecosystem services delivered by Brazilian mammals: spatial and taxonomic patterns and comprehensive list of species. Perspectives in Ecology and Conservation 21:302-310. http://dx.doi.org/10.1016/j.pecon.2023.10.003

Vizcaíno, S. F., R. A. Farina, & G. V. Mazzetta. 1999. Ulnar dimensions and fossoriality in armadillos. Acta Theriologica 44:309-320. http://dx.doi.org/10.4098/at.arch.99-29

Vizcaíno, S. F., & N. Milne. 2002. Structure and function in armadillo limbs (Mammalia: Xenarthra: Dasypodidae). Journal of Zoology 257:117-127. http://dx.doi.org/10.1017/s0952836902000717

Wetzel, R. H. 1985. Taxonomy and distribution of armadillos, Dasypodidae. The evolution and ecology of armadillos, sloths, and vermilinguas (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, DC, USA. http://dx.doi.org/10.1126/science.233.4768.1102

Wilson, D. S, & J. Yoshimura. 1994. On the Coexistence of Specialists and Generalists. The American Naturalist 144:692-707. http://dx.doi.org/10.1086/285702

Wilson, D. E., & R. A. Mittermeier. 2018. Handbook of the Mammals of the World, Vol. 8 Insectivores, Sloths, & Colugos. Lynx Edicions, Barcelona, Spain. http://dx.doi.org/10.25225/fozo.v67.i1.a7.2018